Genetic variation and conservation of the native aspen (*Populus tremula* L.) resource in Scotland.

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Abstract

Increased interest in native woodlands has exposed gaps in our knowledge of our native species. Aspen, (*Populus tremula* L.), one such species, is of considerable conservation value though has been subject to very little previous research. It is widely distributed in Scotland at low density occupying a marginalised niche. Aspen is dioecious but reproduces mainly by asexual means and recruitment is reputed to occur only very rarely. Low population density, a marginal niche and an inability to colonise new sites renders the Scottish aspen resource potentially vulnerable to genetic erosion from natural and anthropogenic disturbance potentially compromising its long term future. Intervention is clearly required. Successful conservation management requires a thorough understanding of genetic structure at the national, regional, and stand scale. The genetic structure of the Scottish native aspen resource was therefore investigated at the national, regional and stand scales using selectively neutral molecular markers.

Isozyme analysis was used to estimate genetic variation and investigate population structure and genetic differentiation in six Scottish aspen populations. Eight systems, yielding eleven putative loci, were employed in screening 275 aspen samples. Genetic variation was shown to be greater than mean values obtained for species sharing similar characteristics, and comparable with the homologous species *P. tremuloides* (P_p=54.5, H_{ep}=0.174, A_p=2.00, A_{es}=0.121) suggesting that no significant loss of genetic variation has occurred. Some inbreeding was detected (f=0.153) and attributed to assortive mating between a small subset of clones retaining sexual function. A small but significant amount of structuring was detected (θ=0.014) although UPMGA clustering of genetic identity (I) indicated little differentiation amongst populations providing little support for a multiple origin hypothesis. It is concluded that the genetic structure in the present Scottish native aspen resource (SNAR) is little changed from the genetic structure in the SNAR when aspen ceased widespread flowering.

The genetic structure of Tomnagowhan Wood, Strathspey, Scotland's largest aspen-dominated woodland, was investigated using the same suite of markers. 186 aspen were sampled, mapped and genotyped in an area of 4.6 ha. Twenty-one clones were identified using a combination of isozyme analysis and probability theory. Clonal diversity in large aspen stands would appear much greater than is often asserted. A wide variety of clone sizes and strategies were also uncovered and leaf flushing date was shown to be an efficient phenotypic clonal marker. Analysis of the distribution of DBH suggests that aspen ramets follow a 'window of opportunity' mode of regeneration with the last burst of regeneration occurring around World War II in Tomnagowhan.

Genotypic diversity in the small relict island aspen population of Orkney was estimated using the same suite of markers. Fifteen aspen locations were sampled. Multi-locus genotyping, probability theory and local knowledge were used to identify 12 independent clones. A review of the literature and legislation on the "safe' minimum number of clones to use in plantations suggests that the twelve Orkney aspen clones are sufficient to be safely used in the expansion of native woodland in Orkney thus enabling only locally derived stock to be used.

The findings of the three surveys are discussed within an ecological and historical context providing a basis for recommendations for the future management and genetic conservation of the Scottish native aspen resource including guidelines on the conservation of the existing resource, expansion of the resource, the production and deployment of aspen planting stock, and strategic initiatives.

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Glossary of Abbreviations.

DBH	Diameter at breast height
DNA	Deoxyribonucleic Acid
EC	European Community
EPS	Effective population size
FA	Forestry Authority
FC	Forestry Commission
FRMR	Forest reproductive material regulations
ha	Hectare
H_0	Null hypothesis
LES	Leaf emergence score
MFST	Millennium Forest for Scotland
mtDNA	mitochondrial DNA
MVP	Minimum viable population
NGO	Non-governmental organisation
NPS	Native Pinewood Scheme
NNR	National nature reserve
NVC	National vegetation classification
NWDG	Native woodlands discussion group
PCR	Polymerase chain reaction
RAPD	Random amplified polymorphic DNAs
rDNA	Ribosomal DNA
RFLP	Restriction fragment length polymorphism
scnDNA	Single copy nuclear DNA
SGE	Starch gel electrophoresis
SSSI	Site of special scientific interest
UPMGA	Unweighted pair group method with arithmetic averages
VNTR	Variable number tandem repeat
WGS	Woodland Grant Scheme

Author Declarations.

I declare that this thesis, submitted for the degree of Ph.D, has been entirely composed by myself, and that all work described and contained within this thesis was carried out solely by myself. No part of this thesis has been submitted for any other degree or professional qualification.

signed,

Eric P. Easton B.Sc. (Hons.)

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Chapter One - Introduction.

1.1 Context

The last fifteen or so years have witnessed a growing interest in, and appreciation of, native woodlands in Scotland (Magnusson, 1994; Peterken, 1996). Initially the main impetus behind the rising profile of native woodlands came from, amongst others, the many individuals that constitute the Native Woodland Discussion Group (NWDG) and such conservation-minded organisations as Reforesting Scotland, who recognised that the native woodland resource in Scotland required positive intervention to secure its long term future and the many multiple benefits associated with it. By 1985 the Forestry Commission had also begun to accept the value of native woodlands and the need for intervention and consequently introduced policies designed to promote informed management of existing semi-natural woodlands and the creation of new native woodlands (Forestry Commission, 1985; 1989). At first much of the attention, both in terms of policy and research effort, was focused on the Caledonian pinewoods but this eventually broadened to encompass broadleaved native woodland (Rodwell and Patterson, 1996). In the last five years the need for management of existing semi-natural woodlands and establishment of new native woodlands has been widely accepted into the forestry mainstream leading to, what Peterken has termed, 'the age of consensus' (Peterken, 1996). This can perhaps be considered to have been formally marked by the inception of the Millennium Forest for Scotland Trust (MFST) which aims to establish a network of new native woodlands across Scotland funded in part by the Millennium Commission but relying on co-operation among landowners, forestry companies, communities, NGOs, Forest Authority and Scottish Natural Heritage.

In parallel with this growing interest in the conservation of native woodlands for their own sake has been a general movement away from production-oriented forestry towards multi-objective forestry. It is now widely accepted that woodlands can supply a number of benefits in addition to timber production and that such benefits are desirable (cf. Forestry Commission, 1991; 1992a; 1992b; 1992c; Hibberd, 1991) There are now a handful of semi-governmental initiatives throughout Scotland, such as the Central Scotland Countryside Trust and Highland Birchwoods, which aim to establish large areas of multi-objective woodland for landscape, amenity, income and nature conservation benefits

(C.S.C.T., 1995). In addition many local authorities and estate owners are recognising the value of multi-objective woodlands (and the value of Woodland Grant Scheme (WGS) payments, particularly the Community Woodland Supplement). In most instances the use of exotic species cannot be justified when production is not the priority, and native species are preferred to secure important nature conservation and landscape benefits. Indeed, of all the proposals for WGS grant submitted to the Forestry Authority between June 1991 and November 1992 almost 95% of broadleaved trees proposed for planting were British native species (Rodwell and Patterson, 1996).

The burgeoning interest in conservation of our native woodlands and the increasing deployment of native species in multi-objective forestry has focused attention onto our native sylva. This growing attention is highlighting many gaps in our knowledge of our native species. British forest science has, for sound economic reasons, tended to focus on high yield exotics neglecting most of native species with the occasional exception of Scots pine and oak, and more recently birch (Ennos, Worrell and Malcolm, 1997). For many of our native species our knowledge of their basic ecology, reproductive biology, post-glacial history, population genetics, and silviculture is limited. Such a paucity of information on these basic aspects our native species may compromise the success of efforts to establish authentic new native woodlands, conserve the genetic resources within our native tree populations and ultimately secure the long term future of our native tree resource.

1.2 Scottish native aspen (*Populus tremula* L.) resource.

Aspen (*Populus tremula* L.) is one of our native species which has been the subject of very little research, indeed, Worrell (1995a) states that less is known about aspen than any of our other native tree species and writes:-

> "Considerable research effort is required before our knowledge of aspen in Scotland can be brought up to the same standard as that of other tree species"

Until Worrell's recent review of the ecology and silviculture of the Scottish native aspen resource (Worrell, 1995a,b) only one British research paper has been published concerning aspen's ecology (MacGowan, 1992), one paper on its silviculture (Powell, 1957) and two on its propagation (Gray, 1949; Hollingsworth and Mason, 1991).

Aspen is Scotland's only native poplar, its characteristic 'jaggy' form, distinctive leaf colouring in Spring and Autumn, and trunk colouring in Winter make a significant contribution to Highland landscapes. Moreover, it is a species of high conservation value significantly enriching the biodiversity of native woodland it occurs in and maintaining interesting assemblages of many rare and threatened insect species (MacGowan, 1992; Worrell, 1995a). It should rightly be regarded as a valued member of the Scottish native sylva.

Aspen is distributed widely throughout Scotland from the Borders to Shetland including Orkney and the Western Isles, though is only frequent in the Highlands especially in the aspen 'hotspots' of Strathspey, Upper Deeside and S.E. Sutherland. Elsewhere it distributed at low density and can be hard to find. Large stands of aspen (>1 ha.) are mainly restricted to the aspen 'hotspots' and have a character and composition unique within the British Isles. Aspen is particularly susceptible to browsing and disturbance and, consequently, is frequently found in marginal sites such as screes, cliffs, roadsides and along water courses where browsing pressure is lighter. In common with almost all of the Salicaceae, aspen is dioecious though is reputed to flower infrequently and to rarely regenerate from seed. It has, therefore, a limited capacity for the colonisation of new sites (Worrell, 1995a). Aspen's main mode of reproduction is asexual by means of root suckers and typically occurs in characteristic even-aged clonal groups. Aspen is a very hardy species and is tolerant of almost all soils types except deep peat. It is also tolerant to extreme exposure and short growing seasons (Worrell, 1995b) and it has been suggested that aspen would perhaps be capable of surviving the last glaciation in glacial refugia as has been hypothesised for Scots pine (Kinloch, Westfall and Forrest, 1986; Soutar and Spencer, 1991; Worrell, 1995a).

It is almost certainly true that aspen is relatively more scarce today than in the original forest cover (Worrell, 1995a). The representation of aspen in native woodland has probably been more severely restricted than any other native species in Scottish native woodlands (Worrell, 1995a). In many areas of Scotland, for example Southern Scotland, Lochaber, and Central Scotland, aspen densities are extremely low. The reputed difficulties in recruitment limit the potential for expansion of the Scottish native aspen resource without intervention. This, coupled with the inevitable ongoing loss of clones from both stochastic

and human disturbance, puts the Scottish aspen resource at risk in the medium to long term.

Recently, aspen has begun to receive very much more attention and interest. The Forestry Authority (FA) and Scottish Natural Heritage (SNH) initiated this interest by recognising a clear need for research into the Scottish native aspen resource (Mason, 1993). The FA and SNH jointly commissioned a survey of aspen sites throughout Scotland (Worrell, 1993), and also a review of the ecology and silviculture of the Scottish native aspen resource (Worrell, 1995a, b). The FA also began research into the vegetative propagation of aspen (Hollingsworth and Mason, 1991; Hollingsworth and Mason, 1993) and set up provenance trials in Argyll and Moray to investigate adaptive variation in Scottish aspen populations (Bill Mason *personal communication*). More recently, Christies Elite Ltd, in association with Micro-propagation Services Ltd, successfully developed an efficient micro-propagation method (Muir, 1996). Both Christies-Elite and Alba are now marketing 'native' aspen planting stock and are reporting increased demand (Rodney Shearer *personal communication*). Trees for Life are also engaged in ongoing work on the distribution and propagation of aspen clones in Glen Affric (Alan Watson, *personal communication*).

Worrell's review (1995a,b) highlighted a number of areas of aspen biology where substantial research is required including: woodland dynamics, conservation value, reproductive biology, performance and population genetics. Worrell suggested that studies of genetic variation within the Scottish native aspen resource were required for advising on the protection of the genetic integrity of the Scottish resource and also for locating suitable populations from which planting stock can be derived (Worrell, 1995b). Furthermore, he suggested that population genetic studies are desirable because they may shed some light on the origins of the Scottish aspen resource. Such work would follow Kinloch, Westfall and Forrest's (1986) classic study of the selectively neutral variation in Caledonian pine populations that provided evidence suggesting that the native Scots pine resource is of multiple origin.

1.3 Genetic and genotypic variation within the Scottish native aspen resource.

The management of the genetic resources of our native tree species is increasingly being viewed as an important management objective (Soutar and Spencer, 1991; Ennos, Worrell and Malcolm, 1997; Eriksson, Namkoong and Roberds, 1993; Millar, Ledig and Riggs, 1990; Ledig, 1986; Forestry Commission, 1991; Krutzsch, 1982; Melchior, Muhs and Stephen, 1986; Vidakovic and Jelaska, 1983; Kanowski and Boshier, 1997). The emerging profile of conservation genetics in Scottish native woodlands circles is mainly due to Forrest's pioneering work into the population genetics of native Scots pine populations which underpins the innovative Native Pinewood Scheme (NPS) (Forrest, 1980; 1982a; Kinloch, Westfall and Forrest, 1986; Forestry Commissior 1989). This scheme seeks to promote the conservation of Caledonian pine woods through the sound management of existing woodlands and the establishment of new native pinewoods whilst introducing steps to conserve the genetic variation within and among native Scots pine populations. Forrest's work introduced to foresters, conservationists and countryside managers the basic concepts of population genetics and began to engender an appreciation of the importance of conservation genetics. As interest and attention have broadened to include all native woodland types and all native tree species the need for good quality information concerning the genetic variation within and among our native tree populations is increasingly becoming evident (Ennos, Worrell and Malcolm, 1997).

There are two main approaches to the evaluation of genetic resources within a population or collection of populations (Ennos, 1996; Eriksson, Namkoong and Roberds, 1993; Newbury and Ford-Lloyd, 1997): estimation of adaptive genetic variation (selectively important variation) and estimation of selectively neutral genetic variation (what Avise (1994) terms molecular marker variation). Adaptive variation is manifest as directly measurable variation in traits such as phenology, disease resistance, growth rate, morphology and performance. Patterns of adaptive variation are, by definition, generally governed by natural selection and usually considered to be under polygenic control (Ennos, 1996; Lawrence and Marshall, 1997). Estimation of adaptive variation over a large number of traits within and among populations can give an idea of the adaptive potential within each population and the extent of local adaptation amongst the sample populations

(Ennos, 1996; Ennos, Worrell and Malcolm, 1997; Stern, 1970). Adaptive variation is generally investigated in forest trees using provenance trials where a large number of usually open-pollinated families from a number of populations are grown in a common environment (Allard, 1970). With the environment standardized the measured phenotypic differences within and among individuals, within and among families and within and among populations can be attributed to genetic variation. Estimation of adaptive variation is most useful in provenance choice and detecting valuable local adaptations (Ennos, 1996).

There are, however, a number of drawbacks that have militated against widespread surveying of adaptive variation in tree populations. As most of the traits are under polygenic control it is difficult to derive standard genetic diversity parameters which can be used for comparison with other populations and species not included in the provenance trial (Newbury and Ford-Lloyd, 1997). Levels of genetic diversity cannot be determined directly from natural populations - reproductive material, either seeds, cuttings or suckers, requires to be collected and grown on in experimental plots. To adequately investigate adaptive variation a number of plots are required sited throughout the geographic range of the populations of interest to account for genotype/environment interactions. Moreover, useful adaptive traits may only be expressed after several years of growth. The costs involved, both in money and time, are usually prohibitive for most genetic conservation programmes and extensive provenance trials are rarely established in Britain except for high yielding exotic species (Ennos, 1996).

Selectively neutral variation in contrast has, by definition, little influence on phenotype (Avise, 1994; Newbury and Ford-Lloyd, 1997; Ennos, 1996). It can only be detected using molecular markers such as isozymes, which allow variation in gene products to be detected, or RFLPs that uncover variation in the DNA itself (Ennos, 1996; Avise, 1994). Since such variation is exempt from selection the patterns of variation detected using molecular markers can be interpreted in terms of non-selective evolutionary processes such as gene flow, genetic drift, inbreeding, history and linkage disequilibrium. By using a stratified sampling strategy and appropriate statistical tools the genetic structure of plant populations at different levels can be investigated: genetic variation within individuals, genetic variation within populations, genetic variation among populations and total genetic variation can be partitioned (Ennos, 1996). Estimates of genetic variation at these levels are described using standard parameters that allow valid comparison with other studies

(Avise, 1994; Hamrick, Linhart and Mitton, 1979; Hamrick, Mitton and Linhart, 1981; Hamrick *et al.* 1991; Hamrick, Godt and Sherman-Broyles, 1992). Indeed, since molecular markers only estimate genetic variation within a sample of the genome such estimates of genetic variation can only be treated as *relative* estimates and must be interpreted within a comparative context to be at all meaningful.

Estimates of selectively neutral variation have been extensively used as measures of the 'genetic health' of populations considered to be under threat (Avise, 1994; Avise and Hamrick, 1996; Newbury and Ford-Lloyd, 1997; Frankham, 1995; Barrett and Kohn, 1991). It is a relatively quick and inexpensive method of surveying genetic resources, indeed, rather than collecting seeds and establishing field trials all that is required of the populations under study are small tissue samples. Many populations can be screened in matter of few weeks rather than the years required for surveys of adaptive variation. However, care must be taken in using selectively neutral variation as a measure of the adaptive potential of a population as selection can only create new adaptations from heritable phenotypic variation. Patterns of selectively neutral variation do not necessarily correlate closely with patterns of adaptive variation as they are influenced by different factors (Ennos, 1996; Frankham, 1995). Nevertheless, selectively neutral variation can be indicative of the limiting effects of gene flow, inbreeding and genetic erosion in general, all of which can act to decrease *both* selectively neutral and adaptive variation within a population and therefore its adaptive potential. Providing estimates of selectively neutral variation are interpreted within a comparative context provided by similar studies of large healthy populations, surveys of molecular marker variation can be useful in determining whether populations are genetically depauperate or not.

The mating system can also be investigated using molecular markers (Ennos, 1996; Avise, 1994; Burke, Rainey and White, 1992). Inbreeding and linkage disequilibrium can be estimated by analysing genotype frequencies derived from population surveys using appropriate markers. A more sophisticated understanding of the mating system can be achieved by fitting obtained genotype frequencies into appropriate mating system models (Brown, 1989). In-depth knowledge of the mating system of a species, especially a threatened species or population can be extremely important when formulating strategies for successful conservation management.

Providing a stratified sampling system and suitable analysis tools are used it is possible to estimate among-population genetic variation (Ennos, 1996). Comparatively large estimates of among-population variation are indicative of genetic differentiation among the individual populations. This differentiation can occur by genetic drift due to small effective population sizes and/or restricted gene flow. Estimation of among-population genetic variation allows the relative importance of ecological factors such as population fragmentation and isolation in determining the structuring of total genetic variation to be evaluated. Differentiation among populations can also indicate the multiple origin of the populations under examination (Ennos, 1996). Kinloch, Westfall and Forrest (1986) demonstrated, using both monoterpenes and isozyme analysis, that the Wester Ross populations of Caledonian pine (*P. sylvestris)* are genetically distinct from other Caledonian pine populations. They interpreted this, together with strong palynological data, as evidence of an independent origin for Wester Ross populations of Caledonian pine.

Molecular markers are also of use in surveying genotypic variation at the stand scale. In a clonal species such as aspen information on the genotypic diversity, extent of clones and clonal strategy is exceedingly useful to guide re-creation of authentic new native aspen woodlands. Molecular markers can be used to identify and delineate individual clones. By mapping all sampled ramets within a stand and then overlaying the genotype derived from screening with molecular markers patterns of clonal spread can be uncovered. Moreover, good clonal molecular markers can be used to produce an inventory of genotypic variation in small relict populations and potentially as markers to be used in the management of genotypic resources in nurseries.

1.4 Objectives.

In the broadest sense this study aims to gain an insight into the genetical, ecological and historical factors which have acted to shape the genetic structure of the present Scottish native aspen resource in order to better inform the genetic management and conservation of this hitherto undervalued and under-researched resource. More specifically, this study seeks to investigate, using isozyme markers, the distribution of selectively-neutral genetic variation at the national, regional and stand scales and in the small relict island population on Orkney. A number of key questions are asked including:

1. Is the Scottish native aspen resource genetically depauperate compared to larger healthier populations and so potentially at risk in the medium-to-long term?
2. Is there any population genetic evidence to support the hypothesis that the Wester Ross aspen population (or any other Scottish aspen population) has an origin independent of the other Scottish aspen populations?
3. Is their any genetic differentiation amongst the Scottish aspen populations which may be indicative of geographical variation in the ecological, genetical or historical factors bearing on them?
4. Are large semi-natural aspen-dominated stands dominated by relatively few clones or are they genotypically diverse?
5. What clonal strategies are adopted by aspen in Scotland?
6. Are there any phenotypic characteristics that could be used as accurate phenotypic clonal markers?
7. Does the small native aspen population of Orkney maintain within it sufficient genetic and genotypic variation on which to base an expansion of aspen woodland area (and, therefore, an increase in population density) throughout the Orkney Islands without a significant increase in risk of disease over the medium-to-long term from pest and pathogen attack?

These questions, and a number of auxiliary questions, are addressed through a series of surveys of selectively-neutral genetic variation made using a suite of isozyme markers.

The first survey, described in Chapter Four, aims to produce estimates of the selectively-neutral genetic variation maintained within the Scottish native aspen resource at both the national and regional (population) scales. It is modelled on previous surveys of neutral genetic variation in Caledonian Pine (Forrest, 1980, Kinloch, Westfall and Forrest, 1986). The precise objectives of this survey are as follows:-

- to produce an estimate of the selectively-neutral genetic variation maintained within the Scottish native aspen resource. To compare this estimate within an appropriate comparative context in order to determine whether the SNAR has undergone significant genetic erosion perhaps due to low population density, the marginal niche now occupied by aspen in Scotland, or the reputed rarity of recruitment from sexual reproduction.
- to produce estimates of selectively-neutral genetic variation within six aspen populations sampled from throughout mainland Scotland. To compare the mean

within-population estimate of genetic variation with other appropriate populations and to compare the within-population estimates with each other to determine whether individual populations have suffered genetic erosion disproportionately due to geographic, genetic, historic or population density factors.

- to produce an estimate of among-population genetic variation from amongst the six aspen populations sampled. To compare this estimate of among-population genetic variation within an appropriate comparative context to evaluate the importance of genetic drift, gene flow, post-glacial history and inbreeding in shaping the present genetic structure of the SNAR.
- to calculate the genetic distance among populations and produce a UPMGA dendrogram in order to visualise the relationships among populations. Differentiation of the Wester Ross population from the others could be interpreted as evidence of an independent origin for this population as has been tentatively mooted (Worrell, 1995a; Soutar, 1991).
- to determine the extent of inbreeding within the SNAR by comparing empirically derived genotypic frequencies with Hardy-Weinberg expectations. Comparison with other studies should allow the importance of inbreeding in shaping the genetic structure of Scottish aspen resource to be evaluated.

The second survey, described in Chapter Five, aims to provide an accurate estimate of the number, size and extent of aspen clones within a sample area of a large, semi-natural aspen-dominated stand in Strathspey, Scotland. An understanding of the genetic and genotypic diversity maintained within semi-natural aspen-dominated woodlands is essential if these woodlands are to be maintained through sound conservation management or if authentic new-native woodlands are to be recreated. A further aim is to investigate the accuracy of a phenotypic marker - flushing date - in identifying and delineating aspen genotypes. As molecular marker technology is not generally accessible to field biologists, foresters and nurserymen it would be advantageous to possess a method for discriminating among aspen clones using easily scorable phenotypic characters. The precise objectives are as follows:

- to estimate the genotypic diversity maintained within a sample stand of aspen dominated woodland in Strathspey.

- to plot the multilocus genotypes onto a stand map allowing the size, shape and clonal strategy of aspen clones to be uncovered.
- to evaluate the accuracy, efficiency and practicalities of using leaf flushing date as a phenotypic clonal marker relative to isozyme markers.

A third survey, described in Chapter Six, has as its main aim the compilation of an inventory of the genotypic variation maintained within the small relict aspen population of Orkney. At present efforts are underway to re-establish native woodlands throughout Orkney which are authentic in terms of species composition and structure and which are established from planting stock of authentic local origin. This survey aims to use isozyme markers to estimate the genotypic diversity within the present Orkney aspen resource to provide a basis on which to gauge whether there is sufficient genotypic diversity in the base population from which to safely expand the present aspen resource without increasing the risk of pest and pathogen attack. The precise objectives are as follows:

- to sample all known aspen clones on Orkney and to estimate the genotypic diversity within the Orkney aspen resource.
- to evaluate whether the number of genotypes present within the Orkney population is sufficiently large on which to base a significant expansion of the resource and hence increase aspen density without significantly increasing the risk of pest and pathogen attack.
- to produce an inventory and map of the aspen genotypes maintained within Orkney to allow efficient collection of vegetative material from which to propagate planting stock.
- to investigate the genotypic variation within small aspen groups on Orkney.
- to estimate the genetic variation within the Orkney aspen population and to compare it with that estimated in mainland populations.

The three main empirical chapters (Chapters Four, Five and Six) together present an integrated approach to the evaluation of the selectively-neutral genetic variation within the Scottish native aspen resource. Genetic variation and genetic structuring are investigated through a range of scales of pattern - from individual small groups of aspen, to a large stand of aspen-dominated woodland, to the regional scale and up to the national scale - to produce a comprehensive picture of the population genetics of Scottish aspen. Throughout a

common set of isozyme markers are employed and genetic variation is expressed through a common set of parameters.

1.5 Thesis structure and layout.

This thesis is set out in nine chapters. Following this introduction are two review chapters; Chapter Two consists of a review of the biology and ecology of the Scottish native aspen resource whilst Chapter Three discusses the diverse range of molecular markers available to ecological geneticists and argues that isozyme analysis using starch gel electrophoresis provides the best all-round genetic marker technique for the particular questions being asked. The next three chapters form the empirical core of the thesis and describe, in turn, the three surveys discussed above. These three central chapters are written in the style and follow the conventions required for a scientific paper and can therefore stand alone. Chapter Seven discusses the findings from these three surveys within an ecological, genetical and historical context to produce a coherent, though necessarily, provisional portrait of the Scottish native aspen resource. Chapter Eight sets out recommendations for the general conservation and genetic management of the Scottish native aspen resource based partly on the findings of this study but also on good conservation practice. Chapter Nine is a short chapter presenting some closing comments.

Chapter Two - Review of the Biology of the Scottish Aspen Resource.

2.1 Introduction.

The autecology of aspen has been subject to very little academic interest and research. Only one research paper has been published on aspen's ecology in Britain, one on its silviculture and two on its propagation (Worrell, 1995a). Indeed Worrell (1995a) states that "less is known about aspen in Britain than probably any other major tree ...". Much of the information available in the literature is in the unfamiliar languages of the Scandinavian, Baltic and Slavic countries where aspen is a commercial species and so deemed a subject worthy of study. In preparing this review I have had to draw heavily on the reviews of Worrell (1995a, b) who managed to secure translations of many papers from small journals of restricted distribution to write the only comprehensive review of aspen's biology in Scotland to date. Although Worrell's work is cited many times in this section additional information is included from papers not cited by Worrell, from conversations with individuals met during the study with considerable knowledge of aspen in Scotland, and from observations made by myself which it would be inappropriate to include in any other section.

2.2 Systematics.

Poplars *Populus* and Willows *Salix* together form the family *Salicaceae.* All species within the *Salicaceae* are trees or shrubs and all are dioecious (except *Populus lasiocarpa* Oliv.) with small wind-dispersed seeds on long cotton-like filaments termed *pappus* (Mitchell, 1974). The genus *Populus* contains around thirty species which are divided amongst five sections. The aspens and white poplars are collected together in the section *Leuce* which is further divided into two sub-sections *Albidae* containing the white poplars, and *Trepidae* containing the aspens.

Family:	Salicaceae
Genus:	*Populus*
Section:	*Leuce*
Sub-section:	*Trepidae*

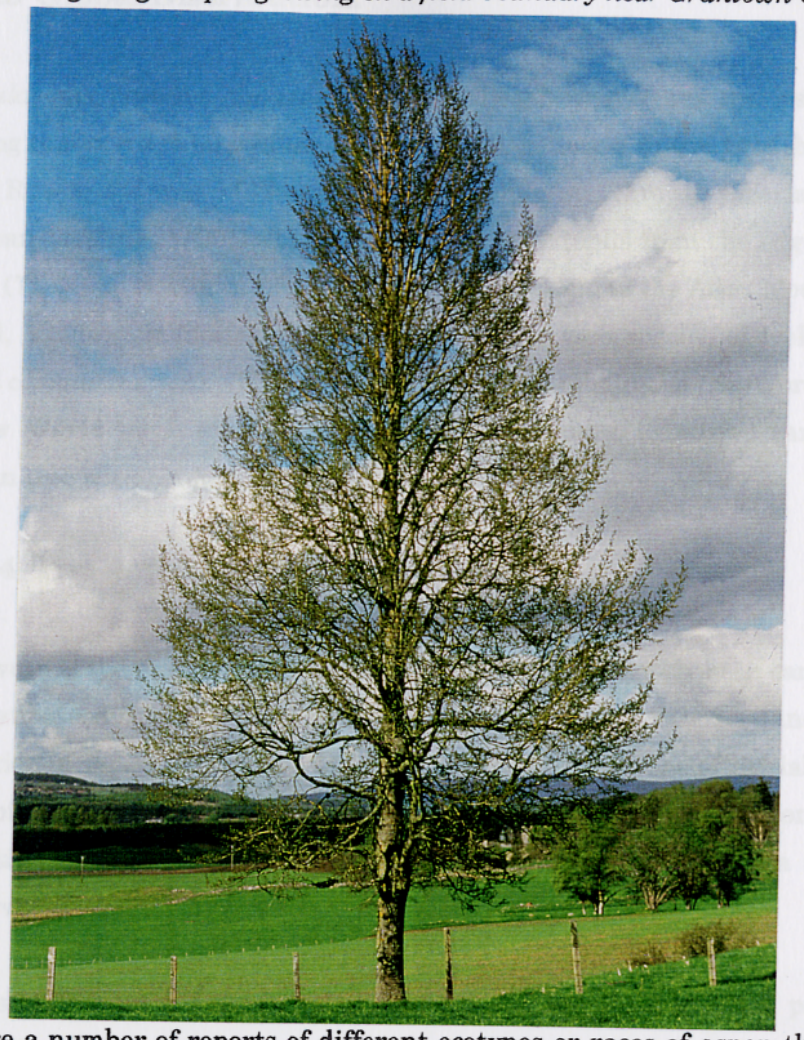
There are five aspen species: *P. adenopoda* Maxim. (Chinese aspen) is found in Central and Western China, *P. sieboldii* Miq. (Japanese aspen) is found only in Japan, *P. grandidentata* Michx. (the large toothed aspen), and *P. tremuloides* Michx. (the trembling aspen) are both North American species, and *P. tremula* (the European aspen), the most widely distributed of all, is native to Europe, Western Asia and North Africa (Jobling, 1990). Henceforth *P. tremula* will be referred to simply as aspen.

Only two poplar species are native to Great Britain: *P. nigra* L. (Black Poplar) is native only to England and although it is widely planted it is rarely found occurring naturally, *P. tremula* is Scotland's only native poplar species (Jobling, 1990; Mitchell 1974).

Three geographical varieties of aspen are recognised, *P. tremula* var. *globosa* Dode and *P. tremula* Var. *davidiana* (Dode) Seheid are both found in China and are sometimes treated as separate species whilst the third *P. tremula* var. villosa *(Lang)* Wesmael is a lowland form found in western and southern Europe and has similarities to the aspen found in Britain (Worrell, 1995b). A pendulous variety *P. tremula* var. *pendula* Jaeg. has also been described and a further form has been reported from Sweden sharing the erect form of the Lombardy poplar (Jobling, 1990; Worrell, 1995b). Three horticultural varieties are also propagated: 'Pendula', 'Erecta' and 'Purpurea'.

There have been a number of reports of giant aspen in Sweden, Latvia and Estonia. Giant aspen have unusually large leaves, vigourous shoots, superior growth rates and increased resistance to rot. They have been found to be triploids bearing 57 chromosomes instead of the more usual 38. The initial expectation that giant aspen could provide a useful commercial opportunity has faded as research has shown that hybrid aspen are a more useful commercial prospect (Börset, 1970). It has been claimed that giant aspen have been discovered in Suffolk and Essex though their ploidy level has not been investigated (Rackham, 1980). There are a number of especially large aspen in Sutherland (in excess of 75 cm. D.B.H.) and although they do not share the characteristic large leaves and vigourous shoots of Baltic giant aspen, it would be interesting to investigate the number of chromosomes of these unusually large specimens.

Fig. 2.1 A large single aspen growing on a field boundary near Grantown-on-Spey.



There are a number of reports of different ecotypes or races of aspen throughout Europe (Worrell, 1995b). Differences between lowland and mountain races have been observed in France, Switzerland and Russia. In France the mountain ecotype is very straight-stemmed with large smooth leaves and shows early self-pruning, whilst the lowland form is inclined to be crooked, with a flattened crown and small leaves and tends to retain dead branches for many years (Silvy-Leligois, 1949 cited in Worrel, 1995b). In Switzerland two races have been described; a mountain race with smooth bark and straight stems, and a lowland race with rough bark, poor form and thick branches (Ceschi, 1970 cited in Worrell, 1995a). The heritability of these distinct phenotypes has not been investigated and may simply be due to the influence of environment. In Scotland, no discernible ecotypes or races have been observed or reported.

2.3 Global Distribution.

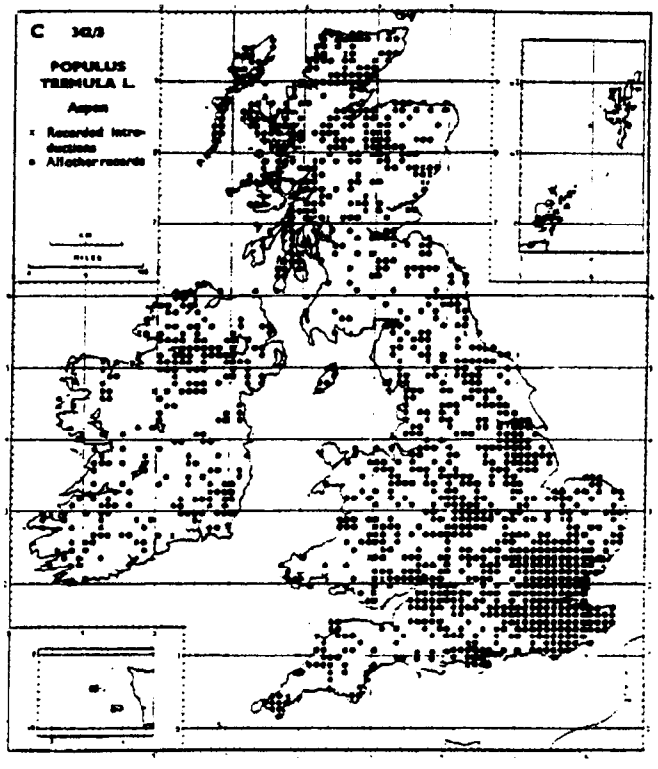
P. tremula has, perhaps, the most extensive distribution of any species in the world even exceeding that of Scots pine *Pinus sylvestris* L. It is native to the British Isles, continental Europe, Russia and most of Western Asia extending east through Siberia to the Bering Sea and Japan (Jobling, 1990). Its latitudinal range extends from the edge of the tundra in Norway (71°N) to Northern Africa where it can be found in the Atlas Mountains of Morocco (Worrell, 1995a). It is also one of the few native tree species of Iceland (T. Benedikz, *personal communication*). This immense range throughout the Old-World is paralleled in the New World by *P. tremuloides* which has the most extensive range of any North American tree species (Jobling, 1990).

2.4 The Aspen Resource in Scotland.

Two surveys of the present Scottish aspen resource have recently been carried out with each investigating a different aspect of the distribution of aspen in Scotland. Of course, the distribution of aspen has previously been published in the Atlas of British Flora (Botanical Society of the British Isles, 1962) - see Fig 2.2 however it gives, in common with all its distribution maps, no indication of the amount of aspen in each area and, compared to later surveys, is visibly incomplete.

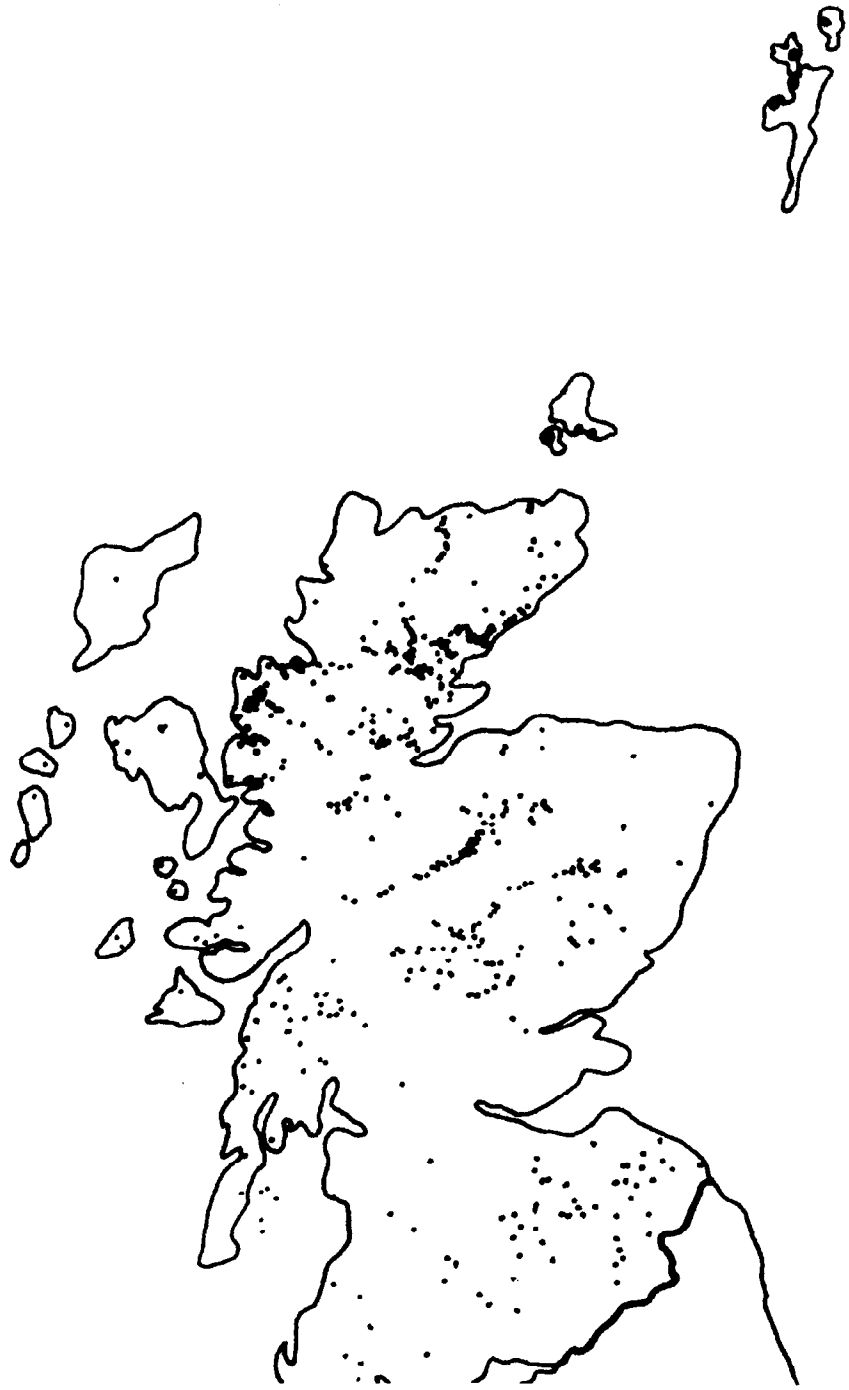
Worrell's (1993) survey, commissioned by S.N.H. and F.A., is based partly on his own investigations but is mainly comprised of submitted reports from foresters, SNH field staff and local naturalists. This survey attempts to collect all aspen reports from extensive aspen-dominated stands to single isolated trees. A total of 647 aspen locations were reported complete with aspect, altitude, and, in some cases a short description. This survey underpins much of this present study. In the course of the present study many more aspen locations were added to Worrell's original list especially in areas where no aspen enthusiasts lived such as Wester Ross. Fig 2.3 shows the distribution of aspen as surveyed by Worrell (1993).

Fig 2.2 The distribution of aspen throughout the British Isles from the Atlas of the British Flora (Botanical Society of the British Isles, 1962).



It can be seen from Fig. 2.3 that aspen is an extremely widespread species in Scotland occurring in every county including the Western and Northern Isles, however, throughout most of the country it is found at very low density. It is only in the Highlands that aspen becomes common and even then it is common only very locally. There are three main aspen 'hotspots' in Scotland where aspen occurs at higher densities and where medium-to-large stands can be found - these are Strathspey, Upper Deeside, and S.E. Sutherland (Worrell, 1995b; 1993; MacGowan, 1992). In these areas, aspen forms a significant feature of the area's natural heritage where it contributes both to the landscape and to the conservation interest of the area.

Fig. 2.3 Aspen locations in Scotland as surveyed by Worrell (1993).



Elsewhere aspen can be found at reasonably high density in Highland Perthshire, in Central Inverness-shire, Easter Ross and locally in Wester Ross. It is rare in the Borders

and Galloway and found very infrequently in Central Scotland. Surprisingly, aspen is very hard to find in the south-western Highlands. In Argyll and Lochaber many sites where aspen would be expected to be found are inhabited by ash *Fraxinus excelsior* L.

Table 2.1 The main aspen stands in Scotland as identified by the Malloch Society after MacGowan (1992). Approximate stand areas and O.S. Grid references are also given.

District	Site	Area (ha.)	O.S. Grid Reference
Sutherland	Torboll	1.5	NH 74 98
	Achany Glen	4.5	NH 57 98
Wester Ross	Gairloch	5.0	NG 81 74
Easter Ross	Achilty	7.0	NH 42 56
Inverness-shire	Inverfarigaig	3.5	NH 52 23
Nairn-shire	Dulsie	5.0	NH 93 41
	Findhorn Gorge	10	NH 93 42
Strathspey	Dulicht	15.0	NJ 02 28
	Spey Bridge	17.5	NJ 03 26
	Culcreach	8.0	NJ 00 22
	Tomnagowhan	30.0	NH 96 15
	Kinveachy Group	5.0	NH 91 18
	Alvie Group	2.0	NH 86 09
	Invertromie	11.0	NN 78 99
	Creagan Breugach	5.5	NN 74 99
Deeside	Kinnordy	9.5	NO 44 99
	Glen Gairn	3.0	NO 34 99
	Dinnet	0.5	NO 46 97

Prior to Worrell's survey the Malloch Society undertook a survey of aspen-dominated woodlands in the Highlands (MacGowan, 1992). The *raison d'être* of this survey was not primarily to investigate the distribution of aspen woodlands but to locate suitable aspen stands in which to investigate assemblages of saproxylic insects. To that extent, only aspen stands greater than 1 ha. were surveyed. Only 18 stands over 1ha. in area were found with the bulk of these in Strathspey between Newtonmore and Grantown-on-Spey. These 18 stands cover a total area of only 157 ha. with only 25 ha. of this area under any

statutory protection. The locations of the main aspen stands identified by MacGowan (1992) are shown in Fig 2.4 and on Table 2.1.

Fig 2.4 The approximate locations of the large aspen-dominated woodlands identified by the Malloch Society (MacGowan 1992)

2.5 Pattern of Occurrence.

Aspen is most commonly seen in small groups occurring along minor roads throughout the Highlands often extending for up to 50m and consisting, in most cases, of a single clone. Aspen does, however, occur in a wide range of contexts. Single trees or small groups of two or three stems, often clearly identifiable as originating from a common root system, are relatively common. These very small groups are often in sites where conditions are harsh and opportunity for expansion is extremely limited such as on cliffs and ledges and by high mountain burns - generally where no other tree species are found. Elsewhere, aspen can be found as single trees or as small to medium groups or groves of aspen within mixed woodland. Often many of the trees in a small group are around the same age and height indicating a short period of regeneration resulting in a single cohort of trees. Also commonly observed are large mature, over mature or moribund standing aspen surrounded by younger more vigourous growth originating from the older ramet. Less commonly observed are large pure stands of aspen though there are a small number of aspen stands in Strathspey, Deeside and Sutherland.

2.6 Sites

Aspen is most often found in sites where grazing pressure is low or has been low in the past as aspen is considered an extremely palatable species to deer, sheep, cattle, hares and rabbits and regeneration can be completely checked by browsing (Worrell, 1995a; Börset, 1970; Powell, 1957). It occurs along roads and railways and along the banks of streams and rivers especially where the banks are steep and inaccessible to browsing species. Aspen is also found on cliff faces, on steep hills and on screes. Aspen can be widely found growing on sea cliffs and bluffs and other coastal sites often very close to high water mark. It is frequently observed growing on the banks of lochs and reservoirs often amongst large rocks with no discernible soil.

The woods where aspen invariably occur are almost always ancient semi-natural native woodlands which have received minimal management and disturbance. In most cases these woodlands are native mixed-broadleaved woodlands described as upland oak-birch woodlands in Bulletin 112 (Rodwell and Patterson, 1996) and classified as W11 and W17 in the National Vegetation Classification (Rodwell, 1991). Occasionally aspen is found growing with juniper in woodland type W19 an example being at Tomnagowhan Wood, Strathspey. Seldom is aspen found growing in the ash woods (W9) typical of the western Highlands.

Aspen is widely reported as being one of the minor components of native pine woods (Rodwell and Patterson, 1996; Steven and Carlisle, 1959), however, it is rarely recorded within native pinewoods (Worrell, 1993). Indeed, in the course of this study aspen was never found growing within any of the recognised native pinewoods although it was frequently observed on the margins which is consistent with its status as a pioneer species in Scandinavian forests (Börset, 1970).

Aspen is not generally found in recently established native woodlands nor in scrub woodlands that develop on abandoned land. The reason for this is almost certainly due to its limited capacity for sexual reproduction in Scotland and, hence the production of mobile propagules. It is almost wholly absent from policy woodlands as it was not a species considered suitable for planting for amenity or timber when most policy woodlands were being established. It is also absent from commercial forestry plantations and farm

shelterbelts. As most of the woodlands in the Borders and central Scotland consist of commercial plantations, shelterbelts, policy woodlands or recently established scrub, it is not unexpected that few aspen reports were collected from these areas. However, aspen can be found in the small component of ancient semi-natural woodland that remains in these areas although it requires thorough surveying to find it. There are, for example, a small number of inconspicuous aspen clones in ancient semi-natural woodland around Airdrie and Shotts in North Lanarkshire.

2.7 Site requirements.

Aspen has little apparent requirement for specific soil types as it can be found growing successfully on a diversity of soils from heavy clays of neutral-to-alkaline pH to freely draining acidic sands and gravels, although, it performs best on fertile freely drained mineral soils of flushed fine sand/clay morainic material (Jobling, 1990; Worrell, 1995b). On wet, nutrient-poor or shallow soils aspen will grow although the trees may be of poor quality (in forestry terms) and there is a suggestion they will be more susceptible to rot.

In the Highlands aspen is most often associated with gleyed brown earths and surface water gleys (Worrell, 1995b). Many clones of aspen have been noted growing on marginal substrates of rock and scree often with little discernible organic material. Aspen has also been observed growing in standing water and with roots growing into running water. On the coasts of north-west Sutherland, Orkney and Wester and Easter Ross small aspen have been observed growing at or very near to high water mark in sand and on rock faces which are frequently inundated with salt water and are subject to large amounts of salt spray. In one case in north-west Sutherland a small aspen was observed growing below high water mark with its roots in salt water and with bladder wrack wrapped around the base of the stem. Clearly aspen is capable of a high degree of salt tolerance.

Surprisingly, given its tolerance to most soil types, aspen does not fare well on deep peats. At relatively few sites were aspen noted growing on peat. At Berriedale Wood on Hoy,, Orkney aspen is freely regenerating on the mineral soil within a ravine, however, no regeneration is present on the deep peat immediately adjacent to the ravine.

As Worrell (1995a) states the vast geographical and altitudinal distribution of aspen throughout the world indicates that it is a species that can tolerate a wide range of climatic conditions. In Europe it is regarded as a continental species most frequent in the boreal zone and in northern temperate forests (Börset, 1970; Huntley and Birks, 1983). However, aspen's distribution in Scotland indicates that it can grow in the oceanic climate of the Northern and Western Isles and the west coast of Scotland, in the oceanic-boreal climate of the central and eastern Highlands and in sub-alpine climates near the treeline in the Central Highlands (Worrell, 1995a).

In continental Europe aspen has been reported growing at elevations from sea level to 500m in the north and west of its range and from 400 to 1600m in the Caucasus and Alps (Ceschi, 1970, Volkovich, 1983 quoted in Worrell, 1995a) and Powell (1957) reports aspen at altitudes of up to 1900m in the Pyrenees.

Aspen has very modest temperature requirements. It is certainly amongst the most frost hardy of all tree species, Powell (1957) quotes an example of aspen surviving a frost of -40°C in Estonia which killed many other broadleaved species. Worrell (1995a, b) argues that aspen is capable of existing at the tree-line in Scotland given an estimated mean summer temperature requirement of 7.6°C. (Börset, 1970). Indeed that aspen can survive in the harsh and almost constant winds characteristic of Orkney and Shetland suggests that it is capable of surviving the high mean wind speeds found at the tree-line.

Worrell (1995a) presents evidence that aspen is extremely drought hardy (a physiological characteristic not unrelated to frost hardiness) and is more drought tolerant than either ash or birch (Rackham, 1980; Börset, 1960 quoted in Worrell 1995a). Perhaps of all temperate and boreal tree species aspen has the least demanding site requirements. The vast distribution of the species and the variety of sites it occurs on confirm that aspen has wide tolerances to climate, temperature, soil, exposure, water availability and salinity. Consequently there are no areas of Scotland that could be considered unsuitable for the planting of aspen for non-commercial purposes.

2.8 Reproduction

In common with many species of the Salicaceae aspen has two modes of reproduction; sexual reproduction through the production of seeds, and asexual reproduction through the production of root suckers.

2.8.1 Sexual reproduction.

Aspen is reputed to regenerate very rarely from seed in Britain (MacGowan, 1992); in his review of the biology of Scottish aspen, Worrell (1995a) remarked that no reports of aspen regenerating from seed throughout the British Isles could be found. In Norway regeneration from seed is rare enough to attract comment when it occurs (Börset, 1970) and, similarly, in western North America *P. tremuloides* regenerates so infrequently from seed that any occasion of finding such a seedling is considered sufficiently newsworthy to justify publication (Dixon, 1935; Faust, 1936; Ellison, 1943; Larson, 1944; Barnes, 1966). It seems the Trepidae poplars are not given overly to sexual reproduction.

Nevertheless, both Powell (1957) and Brodie (*personal communication*) have suggested that a number of single trees in Strathspey are of recent seedling origin (such trees are often of superior form and growth rate). Worrell (1995a) suggests that the many single, small aspen found high on sea cliffs, screes and mountain crags could scarcely have colonised recently by means other than by seed. Indeed, it is likely that aspen will manage, from time to time, to produce viable seed which may manage to establish albeit infrequently.

All members of the family Salicaceae are dioecious (with the exception of *P. lasiocarpa* Oliv.) with male and female flowers borne in catkins on different trees (Mitchell, 1974; Meikle, 1984). The catkins are easily sexed even at a distance. This is fortunate as often the only flowers produced are located in the crown of the tree and are not easily collected. Male catkins are slighter than female catkins, much less robust and much more flexible when blown in the wind. The stamens are initially coloured bright red before darkening to a deep purple on ripening. Male flowers are ephemeral, they quickly wither and are blown off the tree within two weeks of emerging.

Female catkins are much stouter and much less flexible. Before fertilisation the styles are bright red but rapidly wither either as a result of fertilisation or due to desiccation. In aspen the female flowers continue to develop into fruits even when fertilisation has not taken place although the unfertilised fruits are neither as vivid green nor as plump as fertilised fruits. As the fertilised flowers develop into fruits the catkins swell and become almost rigid, losing, in the process, the furry bracts that lie between individual flowers. The fruits become ripe some three to four weeks after emergence and can be recognised by the white fluffy pappus that emerges when the ripe fruit splits. Fig. 2.5 shows female catkins at various early stages of development.

Fig. 2.5 Female catkins at various early stages of development. Loch Laggan 1996.

Aspen flowering buds differ markedly from vegetative buds both in shape and their position on the spur or twig apex. Flowering buds are almost spherical compared to the sharply pointed vegetative buds. Flowering buds are always auxiliary to the vegetative bud

usually in a cluster surrounding a terminal vegetative bud. Buds are initiated in May just after leaf emergence. Bud differentiation is thought to occur during June when the bud either develops as a leaf bud or a flowering bud. This may be determined by the degree of droughting experienced by the tree during this differentiation period (Philipson, *personal communication*). In July it is possible to determine whether the buds will yield flowers or leaves by their shape. The destiny of the buds can be confirmed by pulling the bud apart to reveal either green proto-leaf tissue or the hirsute, brown proto-catkin tissue.

The precise time of flowering varies throughout Scotland depending on latitude and altitude. Surveys were carried out in the springs of 1994, 1995, 1996 throughout Strathspey to determine the dates of flowering and the sex ratio within this population (see - Appendix Five). Flowering was found to begin no earlier than the 14th April with buds continuing to open until early-May. In Sutherland flowering begins around a week later (Boluski, *personal communication*). Male flowers always emerge earlier than female flowers by approximately three to four days although this is difficult to determine because the bursting date of flowering buds is exceptionally variable from clone to clone. By early-May very few male flowers are still visible although all female flowers are still entire. In the early part of the flowering period flowers are often badly damaged by severe frosts. Indeed Brodie (*personal communication*) suggests there may be two waves of flowering, the second occurring in response to late frosts, although no evidence of this was observed during the flowering surveys.

In Strathspey seed begins to ripen around mid-May providing sufficient male and female flowers have been produced to allow pollination to occur. Seed should be collected when the white pappus is clearly visible (Gray, 1949; Worrell, 1995a). The period from the pappus becoming visible to seed being dispersed can be as little as two days leaving a very slim 'window of opportunity' for seed collection.

Over the three years 1994 -1996 when flowering surveys were undertaken 122 putative clones were observed twice weekly throughout the flowering season. In 1994 and 1995 very little flowering was observed at all; only six males and three females were observed in 1994; and only nine males and five females in 1995. However, in 1996 widespread flowering of aspen was observed, a total of 57 male clones and 34 female clones were located. In 1994 and 1995 those clones which did produce flowers produced very few which

were often difficult to reach and consequently sex. In 1996 flowering was exceptionally heavy on almost every flowering tree often to the visible detriment of leaf production later in the spring.

Such heavy flowering was not restricted to Strathspey, extensive catkin production was also reported in Perthshire (Worrell, *personal communication*), and in Sutherland and Wester Ross (Boluski, *personal communication*) and in many other parts of Scotland (Shearer, *personal communication.* There is no suggestion in the literature that aspen flowers periodically like, for example, oak or beech (Worrell, 1995a). As with many tree species flowering often occurs in damaged trees or in damaged branches - so called "agony" flowering. This was observed in many clones which had suffered from wind throw, lost limbs or had root damage due to construction works. The occurrence of this phenomenon may provide the basis for a flowering induction technique perhaps based on the centuries old technique of girdling.

The sex ratio within the Strathspey aspen population was estimated during the spring of 1996 and found to be male-biased at approximately 1.7:1. In other Scottish populations a male-biased sex ratio of this order was also reported (Worrell, Boluski, Brodie, *personal communication*). Throughout Europe aspen sex ratios appear to vary considerably (Worrell, 1995a). In Norway, male:female ratios of 2:1 have been reported (Powell, 1957), whilst in northern Italy ratios of 2.5:1 were found (Gramuglio (1962) cited in Worrell 1995a). In southern Italy and the Caucasus ratios approaching 1:1 were detected (Gramuglio (1962), and Volkovitch (1983) cited in Worrell (1995a).

The sex determination mechanism of aspen is completely unknown as it is in all the Salicaceae . A number of studies have been carried out to determine the presence of sex chromosomes, however, none have successful (Muentzing, 1936; Peto, 1938; Smith, 1943). It is unlikely that sex determination is under chromosomal control, a more likely mechanism is multiple gene control.

Discussion of the factors which influence the infrequency of sexual recruitment in Scottish aspen populations is absent from the limited literature on British aspen. Instead a number of ideas are presented that have arisen during informal discussions with foresters

and forest scientists in the course of this study but particularly at the Native Woodlands Discussion Group.

Infrequent flowering of aspen in Scotland has been mooted as the primary cause of limited sexual reproduction, indeed without flowering sexual reproduction cannot take place. It is certainly widely perceived that aspen seldom flowers in Scotland, indeed it is an occasion of some note when widespread flowering does occur as evidenced by national press reports to this effect (see The Scotsman May 1996). However, a small number of clones seem to consistently flower year after year, clones observed producing catkins in 1994 were also found to flower in 1995 and in 1996. Consistent flowering of a small residual population has also been noted by other dendrologists interested in aspen (Boluski, Brodie, Worrell, *personal communication*). Despite these small number of trees flowering regularly seed is seldom collected from these clones.

Effective pollination is a further prerequisite for sexual recruitment. The relatively low density of aspen clones throughout most of Scotland may act to reduce the potential sources of pollen and also the potential receptors of pollen. To an extent this is countered by the male-biased sex ratio, however, the distance between flowering clones may potentially be too great to allow efficient pollination even in good flowering years. Indeed seed collectors generally only collect from flowering females provided they are adjacent to flowering male trees as it is impossible to determine whether ripe female catkins have been pollinated or not.

Even when seed are successfully and plentifully produced there are other factors which may further confound sexual recruitment particularly at germination and establishment of seedlings. Aspen seed are extremely small and this, coupled with an absence of dormancy, accounts for an extremely limited period of viability outside controlled conditions (Worrell, 1995b). Seed begin to germinate only twelve to eighteen hours after contact with soil (Gray, 1949; Worrell, 1995b; Börset, 1970). Börset (1970) has suggested that unusually exacting conditions are required for successful germination, it is therefore essential that seed are deposited on soils that are immediately suitable for germination during periods of weather that are conducive to successful germination and establishment. Damp, bare soil is required as good contact must be maintained between the radicle and the soil to prevent drying out of the embryonic plant (Gray, 1949). It has been suggested that even heavy rain

droplets may be sufficient to dislodge the small radicle from the moist soil necessary to prevent drying out and death (Gray, 1949). Many aspen seedlings are often lost in periods of hot dry weather immediately after germination which dry up the surface of soils (Börset, 1970). In contrast with many other tree species aspen seed cannot lie in the seed bank until suitable conditions occur for this reason

If seedlings do manage to establish they run the further hazard of the excessive browsing and grazing levels common throughout upland Scotland. Aspen is reputed to be amongst the most palatable of Scotland's native tree species (Worrell, 1995a). Of the 400 aspen sites surveyed throughout this study virtually no natural regeneration of aspen was observed even though evidence of root sucker production was obvious at the majority of sites. The only sites where natural regeneration was obviously occurring were where clones were enclosed by fences preventing browsing animals from accessing the young suckers. Although this example illustrates the effect of browsing pressure on sucker regeneration it also serves to illustrate the browsing pressure that may be attendant on any seedlings that may manage to establish on accessible sites. It is no coincidence that many of the young aspen noted by Worrell (1995a) as perhaps being of potential seedling origin occur on ledges, sea cliffs and other locations inaccessible to browsing animals.

At all stages of the process of sexual recruitment aspen may encounter significant hazards which serve to hamper the natural regeneration of seedlings perhaps more than with other native tree species.

2.8.2 Asexual Reproduction.

In common with most of species within the Salicaceae *P. tremula* shares a capacity to reproduce asexually through the production of root suckers. These root suckers are produced from the characteristically shallow but extensive lateral root system and gradually develop to become independent, though genetically identical, trees. All of the natural regeneration of aspen in Scotland observed in the course of this study was from root sucker origin. A similar situation occurs in Norway, the rest of Scandinavia (Börset, 1970) and continental Europe. In North America almost all regeneration of both *P. tremuloides* and *P. grandidentata* originates from root suckers (Barnes, 1966; 1969; 1975;

Kemperman and Barnes, 1976; Blake, 1963; Cheliak and Dancik, 1982; Cook, 1983; 1985).

This method of reproduction accounts for the distinctive mode of growth commonly observed at many aspen sites throughout Scotland where a single older larger aspen (the ortet in forest parlance) is surrounded by many smaller younger aspen (ramets) derived from the root system of the ortet or parent tree . Figs. 2.6 & 2.7 illustrate the typical growth form of an aspen clone. Often the original tree is long since absent leaving a dense stand of relatively even aged - and genetically uniform - ramets usually referred to as a "clone". Indeed Barnes (1966) has argued that the aspen clone is the most appropriate level at which aspen (both North American and European species) should be managed and, by inference, studied.

Fig. 2.6 A large aspen surrounded by younger ramets on the beach at Gairloch, Wester Ross.

Aspen's lateral root system is extremely extensive, Jobling (1990) quotes examples where aspen suckers have been noted some 40m from the parent tree and further examples of comparable distance have been noted throughout Scotland. Most of the sucker shoots are produced from shallow, thin-barked roots most frequently from those less than 4 cm from

the surface and between 0.5 cm and 2.0 cm in diameter (Börset, 1970). *P. tremuloides* seedlings have been shown capable of initiating sucker shoots during the second year of growth (Barnes, 1966). It is thought that ramets of a clone remain connected to the parent tree and other ramets by the root system for many years. In *P. tremuloides* mature aspen can remain connected to the parent tree for up to 25 years (DeByle, 1964) although no information is available for *P. tremula*.

Fig. 2.7 A mature aspen surrounded by regenerating ramets near Loch Insh, Strathspey.

An extensive aspen root system can survive in the soil for many years with the help of only a few small shoots to sustain it. After clear felling or natural disturbances such as wind throw or fire many aspen suckers can be produced exceedingly quickly in areas apparently devoid of aspen (Börset, 1976 cited in Worrell (1995b). Sucker densities on clear felling mature aspen may fall in the range 15,000 - 70,000 aspen per ha^2 (Börset, 1976 cited in Worrell (1995b) although exceptionally may reach 220,000 aspen per ha^2 (Börset, 1956 cited in Worrell (1995b). Aspen densities in Scotland have been recorded at between 2,500 and 3,700 aspen per ha^2 in 20 - 30 year old stands in Strathspey (Powell, 1957)

2.9 Post Glacial History.

The vegetation history of poplar species in general, and aspen in particular, is poorly understood compared to most other tree species (Huntley and Birks, 1983). This is due to two main reasons: poplar pollen is rather featureless and hence difficult to identify for many palynologists; and, the thin wall of poplar pollen renders it much less durable and more prone to crumpling and deterioration than pollen of other species (Birks, 1970; Huntley and Birks, 1983). As a consequence, poplar species, including aspen, are excluded from pollen diagrams for many areas in Europe. The pattern of the colonisation of aspen into the British Isles is much less well understood than all other native tree species, indeed, aspen is one of the few native species not discussed in Birks' (1989) comprehensive discussion of tree colonisation of the British Isles .

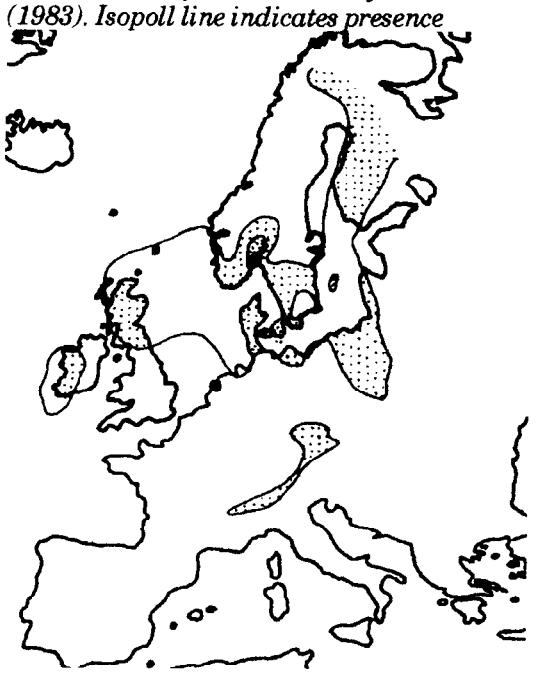
Nevertheless, aspen pollen has been detected in a number of pollen analyses across the British Isles allowing the preparation of isopoll maps showing the distribution of aspen pollen throughout the British Isles for a selection of dates in the Holocene period (Huntley and Birks, 1983). A series of isopoll maps from 10, 000 years B.P. to the present day is presented in Figs 2.8 to 2.14.

Aspen, birch and hazel were amongst the first tree species to colonise the British Isles immediately after the retreat of the glaciers (Worrell, 1995a). Aspen's efficient far-ranging seed dispersal mechanism and its tolerances to poor soils, severe frosts, short growing seasons and exposure must have contributed to its early success. However, as it can be seen in Fig 2.8, the initial distribution of aspen at the beginning of the Holocene (10,000 years B.P.) is disjunctive with two distinct populations: a southern population covering

central England, Wales and central Ireland, and a northern population on the west coast of Scotland stretching from Arran to Wick including the Western and Northern Isles.

Fig 2.8 Distribution of aspen pollen at 10,000 B.P. from Huntley and Birks (1983). Isopoll line indicates presence

Fig 2.9 Distribution of aspen pollen at 9,000 B.P. from Huntley and Birks (1983). Isopoll line indicates presence



On the basis of the present land area of the British Isles these two populations would have been separated by around 150 km however it is possible they may have been joined by a land bridge between Northern Ireland and Kintyre (Birks, 1989). One thousand years later (9,000 B.P.- see Fig. 2.9) aspen pollen is wholly absent from England and Wales although it has colonised most of Scotland except Galloway. At 8,000 B.P. (see Fig, 2.10) aspen pollen is still absent from England and Wales and remains so to the present day; in Scotland aspen pollen is absent from western Inverness-shire though still found throughout the rest of the country; by 6,000 B.P. (see Fig. 2.11) aspen pollen is only detected in Caithness and the Northern Isles. From 4,000 B.P.(Figs 2.12, 2.13 & 2.4) to the present day aspen pollen is absent from any pollen analyses within Scotland save for a trace found in the Central Highlands.

Fig 2.10 Distribution of aspen pollen at 8,000 B.P. from Huntley and Birks (1983). Isopoll line indicates presence.

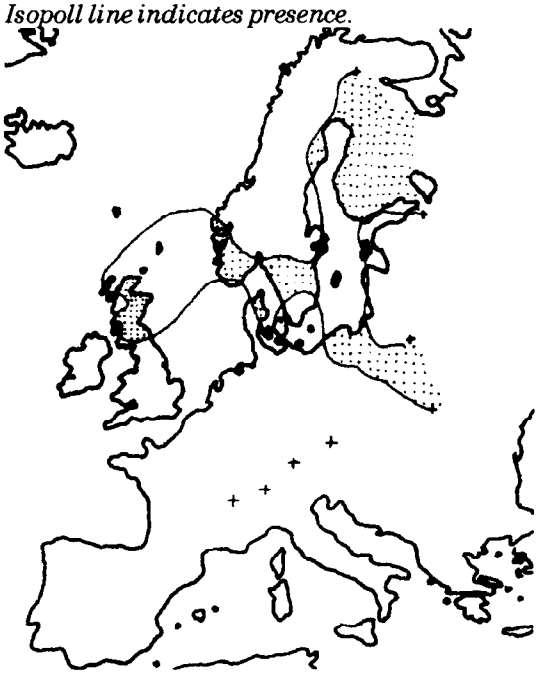
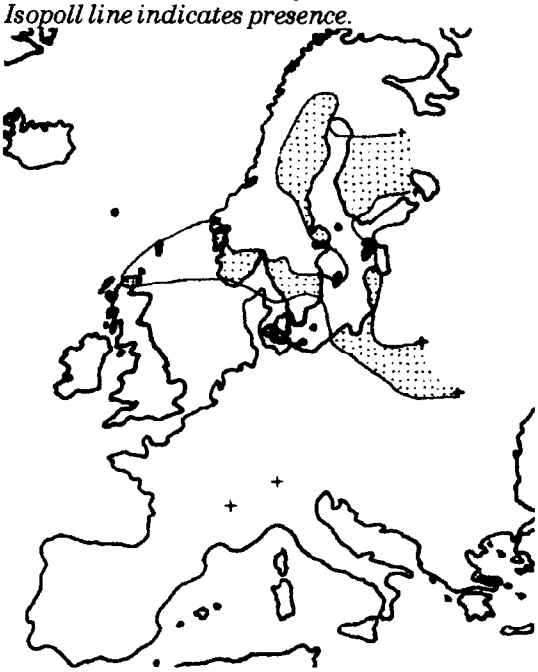


Fig 2.11 Distribution of aspen pollen at 6,000 B.P. from Huntley and Birks (1983). Isopoll line indicates presence.



The disjunct distribution of aspen pollen at 10,000 B.P. inevitably draws parallels to the distribution Scots pine when it was first appeared in the post-glacial pollen record of the British Isles around 8,000 B.P (Huntley and Birks, 1983; Birks, 1989). Scots pine was also found to exhibit a disjunct distribution in its first appearance in the post-glacial pollen profile with a southern population gradually colonising the British Isles from France and a northern population centred on Wester Ross colonising the western Highlands. With no obvious continental origin for this north-western population the distribution has prompted the hypothesis that glacial refugia (perhaps in or around the present coast of Wester Ross) enabled populations of Scots pine to survive the duration of the last glaciation (Kinloch, Westfall and Forrest, 1986; Birks, 1989). This assertion has, to an extent, been supported by evidence from selectively neutral genetic markers, both monoterpenes and isozymes, which indicate that the Scots pine populations in Wester Ross, particularly Shieldaig, are genetically distinct from other Caledonian pine populations in the rest of Scotland (Forrest, 1980; Kinloch, Westfall and Forrest, 1986; Ennos, 1991; Ennos, Sinclair and Perks, 1997). The biology of aspen is such that any refugia that enabled Scots pine to survive the last glaciation would also have allowed aspen (amongst other hardy species) to

survive (Worrell, 1995a; Soutar and Spencer, 1991). It is therefore possible that aspen populations may also have survived the last glaciation in refugia similar to those that harboured Scots pine and managed to colonise the north-western coasts of Scotland immediately after the retreat of the glaciers.

Fig 2.12 Distribution of aspen pollen at 4,000 B.P. from Huntley and Birks (1983). Isopoll line indicates presence.

Fig 2.13 Distribution of aspen pollen at 2,000 B.P. from Huntley and Birks (1983). Isopoll line indicates presence.

There are clearly a number of difficulties in acceptance of the Scots pine glacial refugia hypothesis. The extreme climate, poor soils and physical actions of the icesheet for thousands of years would make conditions well nigh impossible for tree survival (Kinloch, Westfall and Forrest, 1986). It is known that the Gulf Stream, which contributes to the relatively mild climate of north-western Scotland in the present day was offset to the south with a northern boundary about 42°N (CLIMAP project members, 1976). Unglaciated sites would have been few in the north and permafrost and solifluction would have made growing conditions exceptionally difficult on those few ice free areas. Other hypotheses have been put forward to explain the disjunct distribution of Scots pine including jump-dispersal to north-west Scotland from southern Britain, mainland Europe or the North Sea basin from long distance transfer of seeds perhaps by freak winds (Birks, 1989). This hypothesis is all but untestable and unlikely. A third hypothesis put forward is that Scots

pine extended rapidly through western Ireland and south-western Scotland prior to 8,500 BP leaving no pollen traces as it was locally rare being confined by competition to marginal or coastal habitats (Forrest, 1980; O' Sullivan, 1974). However, extensive unsuccessful searches for macrofossils in SW Scotland lead to the conclusion that Scots pine did not cross from Ireland into Scotland through Kintyre, Islay, Jura or Arran (O' Sullivan, 1974). The third hypothesis is also consistent with the distribution of aspen at 10,000 B.P., aspen could have crossed the Irish Sea, which would have been much narrower at the beginning of the Holocene compared with the later period of colonisation of Scots Pine, and colonised the west coast of Scotland where conditions may have been suitable for rapid northerly expansion. However, Kinloch *et al.* (1986) rightly assert that their glacial refugia hypothesis with all its difficulties is easier to reconcile with their palynological and genetic findings than both the jump hypothesis and the Irish invasion hypothesis.

Fig 2.14 Distribution of aspen pollen at present from Huntley and Birks (1983). Isopoll line indicates presence.

The interpretation of the aspen isopoll maps is confounded by the ability of aspen populations to maintain themselves by asexual reproduction by root suckering (Worrell, 1995a). Aspen can only have colonised the British Isles from seed but once established clones can maintain themselves for hundreds or even thousands of years (Jelinski and Cheliak, 1992; Kemperman and Barnes, 1976). Whilst the presence of aspen pollen can be

interpreted as evidence of the presence of flowering aspen in the area at the particular period, the absence of aspen pollen in an analysis can only be interpreted as an absence of male flowering aspen and not, as for other species, a complete absence.

Aspen pollen is undetected in pollen analyses from England and Wales from 9,000 B.P. to the present and absent from pollen analyses in Scotland from 6,000 B.P. (except Caithness) to the present. Yet aspen is found across the British Isles and in some areas is locally common, i.e. Strathspey, Upper Deeside and SE Sutherland. Even in areas where aspen is plentiful aspen pollen is largely undetected in present-day pollen analyses of moss polsters (Huntley and Birks, 1983). Whilst it is highly likely that the abundance of aspen decreased due to the colonisation of large areas of Highland Scotland of Scots pine from 8,000 B.P. to 5,000 B.P. displacing the former broadleaved woodland, and would have also have suffered from the increasing blanket bog formation beginning around 4,000 B.P., and the activities of neolithic Man from around 6,000 B.P. (Godwin, 1975; Huntley and Birks, 1983), such a reduction in abundance would not have completely removed aspen pollen from the pollen profile. A plausible explanation for the absence of aspen pollen in pollen records from the mid-Holocene to the present is that aspen populations ceased flowering and hence sexual reproduction and maintained themselves clonally from root suckers many potentially surviving to the present day. A similar interpretation has been mooted to explain the post glacial history and continued presence of *P. tremuloides* which also produces seed very rarely in Alberta (Jelinski and Cheliak, 1992). However such an interpretation requires a mechanism to account for the cessation of sexual reproduction.

In continental Europe aspen populations regularly flower and produce seed (Worrell, 1995b; Börset, 1970). The isopoll map of present day aspen pollen deposits (Fig. 2.14) indicates that aspen regularly produces significant amounts of pollen in Sweden, Norway, Finland, Germany, Czechoslovakia and France (Huntley and Birks, 1983). The climate in these areas is characterised by hot, dry summers and very cold winters - the Continental climate. The climate of the British Isles is described as Oceanic - cold wet summers and cold wet winters. However, the climate of Britain was not always like this. Before 7,500 B.P., in the Boreal period (as defined by Godwin, (1975)), the climate of the British Isles was similar to the present day continental climate with hot dry summers and cold dry winters (Godwin, 1975). At around 7, 000 BP, at the transition between the Boreal and the Atlantic period, the climate in Britain started to change becoming more oceanic. When

British aspen populations were producing substantial amounts of pollen they did so in a climate similar to that experienced by present day continental aspen populations which also flower regularly.

In a pollen analysis of peat deposits from Abernethy Forest, Strathspey, substantial amounts of aspen pollen were detected until around 7,400 B.P after which it was no longer found (Birks and Mathewes, 1978; Birks, 1970; Rodwell, 1991). The disappearance of aspen pollen has been interpreted as being due to the colonisation of the area by Scots pine displacing the mixed deciduous woodland of which aspen was a constituent. However, it is unlikely that aspen was completely displaced from the area by Scots pine as Abernethy is very heterogeneous and would have supported significant broadleaved woodland on areas unsuitable for pine. Moreover, the other broadleaved species associated with aspen in this deciduous woodland - *Betula* and *Corylus* - did not begin to decline until c.7,200 B.P. some 300 years later. I contend that the disappearance of aspen pollen from the Abernethy record was not completely due to the colonisation of pine and but also associated with the, albeit correlated, climate change interfering with flowering processes to the extent that pollen production largely ceased.

Such indirect evidence that the present oceanic climate is not conducive to widespread flowering of Scottish aspen populations is further strengthened by the heavy and widespread flowering of Scottish aspen populations in the summer of 1996 following the extremely hot and dry summer and cold winter of 1995. Indeed Powell (1957) reports that Scottish aspen only flowers in the summer following a hot dry July. The precise reason for the cessation of flowering in the Scottish aspen population could be elucidated by reciprocal transplant experiments in Scotland and in Finland where aspen flowers frequently.

As has already been argued, in contrast with other species, there is little palynological data to inform us of the aspen resource on past times. The perceived scarcity of aspen in present times and its apparent palatability to browsing species have led to the widespread belief that aspen has declined from 'natural' 'wildwood' levels, whatever they were (Worrell, 1995a). Certainly browsing has been reported as a cause of decline in aspen populations in Norway (Berg, 1946 cited in Worrell (1995a)), moreover, Jobling (1990) has postulated that poplar bacterial canker *Xanthomonas populi* may have accounted for a large decline in aspen populations. However, the most likely reason for any decline in aspen populations is

a combination of man-made disturbance and the inability of aspen to disperse itself into new locations due to the low production of seed. As aspen has had little history of utilisation of its timber it is unlikely that populations diminished due to widespread felling, indeed aspen responds to felling with vigourous suckering. Perhaps more than any other native tree species aspen has suffered *indirectly* from Man's activities. As aspen reproduces mainly through the production of root suckers aspen populations are not, on the whole, very mobile. Consequently aspen clones lost through disturbance are not replaced very quickly by seedlings. From an initial post-glacial recruitment of seedlings clones are gradually been eroded with little recruitment of new clones and hence recolonisation of new sites.

This argument stands in direct contradiction to Rackham (1980) who postulated that present aspen populations in England may be much greater than in the 'wildwood' because there is now much greater disturbance in the countryside allowing populations of pioneer species such as aspen to increase in density. Rackham's argument is flawed because he equates aspen's theoretical status as a pioneer species with an ability to efficiently disperse by seed and to establish quickly. Whilst this may be the case in continental Europe it is far from true in Britain. Aspen does indeed have many of the attributes of a pioneer species however, its inability to effectively reproduce by sexual means precludes it from being characterised as a pioneer species in Britain. His assertion that it could be more common now than in the mythical 'wildwood' cannot be based on anything more than the absence of aspen from the pollen record which he possibly equates with an absence of aspen *per se*.

2.10 Damage, pests and diseases.

Aspen is resistant to low temperatures, drought, water logging, wind throw and resists damage from snow better than birch (Worrell, 1995a) indeed it is an exceptionally hardy species as evidenced by its wide distribution throughout the Old World. Although susceptible to browsing from mammals such as voles, Red and Roe deer, hares, sheep and rabbits when young (Hollingsworth and Mason, 1991) very little damage to established aspen has been noted in the course of this study. There are a number of insect species that feed on aspen, Powell (1957) has listed 27 species which bore in the wood or bark, or feed on the leaves and which commonly occur in British populations. Of these, the most

important are the poplar long horn beetles: *Saperda carcharias* L. feeds on the cambium and wood whilst the smaller *S. populanea* L. feeds on the pith of shoots (Worrell, 1995a). Neither of these species causes anything more than negligible damage to Scottish aspen populations.

Fig. 2.15 Severe bacterial canker Xanthomonas populi *on the trunk of an aspen at Ardgay, Sutherland. Although still growing the form is severely affected.*

Aspen is at most risk from bacterial and fungal diseases, the most dangerous of these is poplar bacterial canker *Xanthomonas populi*. Bacterial canker is a major disease of European commercial poplar plantations and aspen is particularly susceptible, perhaps more so than any other poplar species (Jobling, 1990). It is suggested that most provenances of British aspen are susceptible and Jobling (1990) believes that the local decline of aspen in many areas is due to bacterial canker - both statements are, however, only supposition as no work has been carried out into the resistance or prevalence of bacterial canker in British native aspen populations. Very little incidence of bacterial canker was noted when surveying aspen sites throughout Scotland. Of the 312 sites visited only 7 clones were observed with visible signs of bacterial canker. It may be that

the density of present day aspen populations is too low to maintain parallel populations of bacterial canker.

The disease attacks the tree through small cracks in the bark and acts on the tree to cause large cankers. These cankers can quickly girdle twigs and small branches causing the distinctively shaped crown of a heavily infected tree. On the trunk the cankers take much longer to develop and only in relatively rare cases is the tree killed rapidly through girdling. In exposed situations partial girdling can weaken the trunk leading to wind snap at the cankered point. Infection with bacterial canker in all cases causes loss of form and reduction of growth rate (Jobling, 1990). Fig. 2.15 illustrates the effects of *Xanthomonas populi* on a mature aspen in Sutherland. Although not killed the form of the tree is severely distorted.

There are a number of other diseases of aspen such as *Venturia macularis* which attacks young regeneration, various leaf rusts *Melamspora* spp., canker *Dothichiza populea*, and honey fungus *Armillaria* spp. The importance of these diseases in Scottish, indeed British, aspen populations is yet to be studied though their impact on present day populations is thought to be low.

2.11 Genetic Variation

To date no studies of genetic variation of either neutral markers or adaptive variation have been carried out in Scottish or British populations. Similarly, in continental Europe studies of selectively neutral genetic variation within and among populations are yet to be carried out. However, there have been a number of studies where differences between clones and provenances have been investigated and demonstrated for a wide range of phenotypic characters in populations from throughout Europe[1]. These include: flushing date, autumn colouration of leaves (Baranchugov, 1983 cited in Worrell, 1995a), tree form, stem form and branching habit (Schonbach, 1961, Pauley, 1963, Morhdiek, 1980, Plyura, 1989 all cited in Worrell, (1995a), diameter growth and yield (Morhdiek, 1980, Plyura, 1989 cited in Worrell 1995a), seed characteristics (Gallo *et al.* 1985 cited in Worrell

[1] Many of these studies were published in Scandinavia and the Baltic republics when it was still routine to use their native language. Other studies are of Soviet origin where the normal language of science remains Russian. In this section I have relied heavily on Worrell's reviews (1995a,b) as he had access to translations and translated some himself.

1995a), rooting success of cuttings (Behrens and Melchior, 1978 cited in Worrell 1995a; Hollingsworth and Mason, 1991); resistance to disease (Gallo et al., 1985, Tamm, 1987 cited in Worrell 1995a) and wood density and fibre length (Morhdiek, 1980 cited in Worrell (1995a). Variation in growth patterns has been shown to be related to day length in a large study of provenances collected from a wide latitudinal range in Sweden (Sylven, 1940 cited in Worrell (1995a) and plants from high latitudes with a short growing season were shown to maintain their dwarfed growth form (Pauley, 1963 cited in Worrell (1995a).

Fig. 2.16 The distinctive nature of aspen-dominated mixed broadleaved woodland - Tomnagowhan, Strathspey.

This accretion of information on useful phenotypic traits suggests that large amounts of genetic variation are present European populations over a wide range of characters. This is not unexpected in a species which is so widely distributed and which has such wide tolerances to a wide range of soil, climate and other environmental conditions (Hamrick, Linhart and Mitton, 1979; Hamrick, Mitton and Linhart, 1981; Hamrick *et al.* 1991; Hamrick, Godt and Sherman-Broyles, 1992).

Despite the lack of formal studies of genetic variation in domestic populations a number of casual observations have been made which suggest that there is significant levels of variation within Scottish aspen populations. For instance, clonal and provenance differences in leaf size and leaf colouration, especially at flushing and abscission times, have been noted (Boluski *personal communication*) and clonal differences in the date of flushing and leaf fall have also been reported (Brodie *personal communication*). Although a wide variety of growth form is noted in Scottish aspen populations (Worrell, 1995b), it is more likely that such variation is due to more to environment rather than genotype. Nevertheless populations in Deeside and Strathspey do appear to be particularly straight stemmed with regular fastigiate branching (Worrell, 1995b). Examples of clones potentially resistant to bacterial canker have been observed during this study. At Ardgay, Sutherland a healthy uninfected clone grows immediately adjacent to a badly cankered clone without, it seems, succumbing to infection. Moreover, there appears to be clonal variation in susceptibility to the small black galls often seen on aspen. Some clones seem to be especially prone to these galls and other clones show no incidence of them at all. Adjacent clones have been observed where one clone is free from galls and the neighbouring clone exhibits large numbers of them. The causal agent of these galls is at present unknown.

2.12 The value and importance of aspen in Scotland

2.12.1 Landscape Value.

Aspen has a characteristic crown shape and branching pattern. It has attractive foliage in spring during the flushing period and also in autumn during the period of abscission; in these periods the leaf colour can vary from yellow, through to lime green, dark green, silvery-green to browns and bright reds. The perpetual motion of the leaves, their smell

and their rustling sound also add to the aesthetic appeal of this species. In winter the grey/silver of the bark makes aspen especially apparent, aspen clones can easily be picked out in woodlands especially if they are on a hillside. Indeed it is much easier to find aspen clones in winter than at any other time.

In those areas where there are high density populations of aspen - Strathspey, Upper Deeside and Sutherland - aspen forms a significant and locally distinctive feature of the natural heritage. Around Loch Insh, Loch Laggan, Loch Kinord, Dinnet, Invershin, Loch Shin, Grantown-on-Spey, the Upper Dee, and Boat of Garten aspen clones are especially apparent. The remaining large aspen woods identified by MacGowan (1992) are a woodland type unique in Britain and have a character unlike any other type of woodland - see Fig 2.16.

Fig. 2.17 Aspen in winter on the otherwise barren shores of Loch Naver, Sutherland

In Orkney, the Outer Isles and parts of Wester Ross and north Sutherland aspen is one of the few tree species present and therefore contributes disproportionately to the landscape.

For instance, the large aspen growing along the western banks of Loch Naver are visible for miles; such is the scarcity of native trees and the surprising size of these trees given the latitude -see Fig. 2.17.

2.12.2 Nature Conservation Value.

Research into the nature conservation value of aspen has, in common with many other facets of aspen biology, been largely neglected to date. Only one paper has been published which discusses the conservation value of British aspen populations (MacGowan, 1992). Despite the lack of research, aspen can be considered to be of considerable conservation value for two main reasons: it has an intrinsic value simply because it is a tree species native to Scotland; and secondly, it has an extrinsic value as a consequence of its relatively low population density and the limited area of aspen-dominated woodland. Indeed, Worrell states, in his review of aspen (1995a, b) that:

> "The representation of aspen in native woodland has probably been more severely restricted than other native species, and it merits regeneration and planting on those grounds alone."

Aspen's intrinsic attributes include being an important tree species for woodpeckers and hole nesting birds and having an unusual selection of bird species associated with it (Worrell, 1995a). Aspen is also host to a large number of invertebrate species; over 160 invertebrate species are associated with aspen including 22 Hemiptera, 60 Lepidoptera, 30 Coleoptera and 15 Diptera species (Worrell, 1995a). Sixty invertebrate species are specifically associated with Scottish aspen populations, indeed there is a suggestion that insect communities in Scottish aspen populations are significantly different from English populations (Worrell, 1995a).

A study into saproxylic insects in Scottish aspen populations identified many rare species including one species new to science and seven Red Data Book-listed species (MacGowan, 1992). In MacGowan's study of aspen-dominated woodland he concluded that these interesting insect communities only occurred in large aspen woodlands with a high density of aspen and a wide age range. Aspen also has the ability to return soils which have become podsolised and acidified as a result of deforestation back to their natural state.

The distinctive aspen-dominated woodlands of the Central Highlands are a unique and under-represented woodland type in the British Isles which have been neglected to date as evidenced by the National Vegetation Classification (NVC) (Rodwell, 1991) omitting aspen woodlands as a distinctive woodland type. As the NVC is now treated as the definitive classification of the vegetation of Britain there is a danger that because these woodlands are not recognised as having a unique character and value they will not be managed effectively as *aspen* woods. Forestry Commission guidelines on the management of semi-natural woodlands have been published based on NVC woodland classifications (Rodwell and Patterson, 1996; Forestry Commission, 1995). If these guidelines are strictly adhered to then aspen woodlands may be managed out of existence. There is a case for the inclusion of aspen-dominated woodlands in the NVC and for the F.C. to publish suitable guidelines for the management of this important woodland type.

2.12.3 Timber Value

There is no reported history of commercial aspen timber production in Scotland and therefore no information on likely volume production in Scotland (Worrell, 1995a). Mean annual increments of between 4 and 10 m^3ha^{-1} have been reported in Scandinavia, Russia, Poland and Estonia (Worrell, 1995a; Powell, 1957) which are commensurate with values for other northern hardwoods such as silver birch and alder.

Surprisingly, and in contrast with comparisons of performance with other native broadleaved species, aspen does much less well in Scotland than in Scandinavia (Powell, 1957). Scottish aspen does not, it seems, grow as tall as Scandinavian aspen although comparative girths are achieved. Worrell (1995a) believes there may be grounds to believe that Scottish aspen is intrinsically less vigourous than northern continental populations although this could only be tested by rigorous provenance trials.

Scottish aspen shows mixed form. Certainly many clones in dense stands in Strathspey and Deeside are of good form with little branching and straight stems which are ostensibly rot-free. However, outwith these areas, clones are invariably of poor form. Only in Strathspey and Deeside are large dense stands found on favourable sites; elsewhere aspen is mainly restricted to marginal sites of high exposure and poor soils where good performance could not be expected.

Aspen timber shares many of the properties of other common poplar species (Worrell, 1995a). It is relatively soft, elastic, straight and moves little on drying. Good quality aspen timber can used for many of the same ends as other poplar species such as for packing and pallets. Brodie (*personal communication)* is currently constructing a house using substantial amounts of native aspen timber. Logs of exceptionally good quality can be used for interior panelling although aspen has little grain and makes for a bland finish. It can also be used for fibre board, particle board and pulping and is suited to match-making and veneers. Early aspen plantations in Scotland were set up by Bryant and May in Argyll to determine its potential for match-making in Scotland (D. Malcolm *personal communication*).

Worrell (1995a) states that there are "negligible opportunities for aspen timber production" in Scotland although he agrees it should have a place in new native woodlands and also as a component in coniferous forest. It may also find a place in the specialist hardwood market.

2.12.4 Cultural/Historical Value

The present English name for aspen is derived from the old Teutonic term for poplar, for example, in Anglo-Saxon it is *Aespe*, in mediæval English it is asp. Modern northern European languages also share this derivation - *Espe* in German, *Asp* in Swedish and *Osp* in Norwegian. There are a number of Scots words for aspen including *esp, quakin asp, quakin aish, quakin trei* and *tremmlin trei* (Robinson, 1987; Macleod, 1990) sharing this same root. There are two Gaelic names for aspen *Eubh* and *Critheann* (the shaking tree) Examples of place names derived from Gaelic terms for aspen include Balcreen in Argyll (Planterose *et al. 1991*), and Killiecrankie in Perthshire (coille -wood, crankie - distortion of *critheann*). In contrast with many other native tree species aspen has remarkably little folklore associated with it except as a tree of ill-omen reputedly because its timber was used to fashion Christ's cross (Milner, 1992). Despite this negative association aspen is found surprisingly frequently in Highland gardens. There is little information on the use of aspen in Scotland, although in England, aspen was used in the making of arrow shafts and also in the making of clogs. In Tomnagowhan Farm, Strathspey aspen timber is routinely used by the farmer for sheds, huts and fences though this is, by no means, common.